1 **Production and accumulation of reef framework by calcifying corals and macroalgae on**

2 **a remote Indian Ocean cay.**

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Abstract

Coral reefs face increasing pressures in response to unprecedented rates of environmental change at present. The coral reef physical framework is formed through the production of calcium carbonate ($CaCO_3$) and maintained by marine organisms, primarily hermatypic corals, and calcifying algae. The northern part of Western Australia, known as the Kimberley, has largely escaped land-based anthropogenic impacts and this study provides important metabolic data on reef-building organisms from an undisturbed set of marine habitats. From the reef platform of Browse Island, located on the mid-shelf just inside the 200 m isobath off the Kimberley coast, specimens of the dominant coral (6 species) and algal (5 species) taxa were collected and incubated ex-situ in light and dark shipboard experimental mesocosms for 4 hours to measure rates of calcification and production patterns of oxygen. During experimental light/dark incubations, all algae were net autotrophic producing 6 to 111 mmol O_2 m^{-2} day^{-1}. In contrast, most corals were net consumers of O_2 with average net fluxes ranging from -42 to 47 mmol O_2 m^{-2} day^{-1}. The net change in pH was generally negative for corals and calcifying algae (-0.01 to -0.08 h^{-1}). Resulting net calcification rates (1.9 to 9.9 g $CaCO_3$ m^{-2} d^{-1}) for corals, and calcifying algae (*Halimeda* and *Galaxura*) were all positive and were strongly correlated to net O_2 production. In intertidal habitats around Browse Island, estimated relative contributions of coral and *Halimeda* to the reef production of $CaCO_3$ were similar at around 600 to 840 g m^{-2} $year^{-1}$. The low reef platform had very low coral cover of $< 3\%$ which made a smaller contribution to calcification of ~240 g $CaCO_3$ m^{-2} $year^{-1}$. Calcification on the subtidal reef slope was predominantly from corals, producing ~1540 g $CaCO_3 m^{-2}$ $year^{-1}$, twice that of *Halimeda*. These data provide the first measures of community metabolism from the offshore reef systems of the Kimberley. The relative contributions of the main reef builders, in these undisturbed areas, to net community metabolism and $CaCO_3$ production is important to understand exclusively climate-driven negative effects on tropical reefs.

1. Introduction

The functioning of healthy coral reefs, as some of the world's most biologically (Stuart-Smith et al., 2018) and structurally complex ecosystems (Hughes et al., 2017b), results in a number of ecosystem services. They provide coastal protection, with reef structures acting to dampen wind and wave driven surges (Perry et al., 2018) and support a diverse range of species that provide critically important resources (such as food) for coastal livelihoods (Hoegh-Guldberg et al., 2007). However, coastal coral reefs in the Anthropocene era have been degraded for more than a century by overfishing and pollution (Hughes et al., 2017b). With the current unprecedented rate of environmental change, coral reefs face growing pressures. These range from localised eutrophication (Hewitt et al., 2016) and sedimentation (Hughes et al, 2017a), to larger scale recurrent weather events (marine heat waves; Moore et al., 2012) and rising atmospheric greenhouse gases (especially carbon dioxide, CO_2; IPCC, 2014) that result in increasing ocean temperatures (due to atmospheric heat absorption) and ocean acidification (OA) (Hoegh-Guldberg, 2007; Doney et al., 2009; Perry et al., 2018). Once thought protected by the very nature of their isolation, remote reefs are also now showing impacts by increasing stressors brought about by anthropogenic climate change (Hughes et al., 2017b).

As one of the most important determinants of overall reef function, the construction and maintenance of the calcium carbonate ($CaCO_3$) reef structure (the accumulation of which requires the net production of calcium carbonate by resident taxa; Cornwall et al., 2021) is vital to the myriad of ecosystem services that coral reefs provide (Hoegh-Guldberg et al., 2007; Andersson et al., 2013; Moberg and Folke, 1999). The coral reef physical framework is formed and maintained through the production of calcium carbonate ($CaCO_3$) by marine organisms, primarily hermatypic corals, crustose coralline algae (CCA), and other calcifying algae (Vecsei, 2004; Perry et al., 2008; Perry et al., 2012). Scleractinian corals are primary reef

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builders in tropical environments, producing $CaCO_3$ through skeletal deposition. This net calcium carbonate production is a balance between gross production minus the loss due to physical, chemical, and biological erosion (Cornwall et al., 2021). The net calcium carbonate production and related potential vertical accretion of reefs is increasingly threatened by anthropogenic climate change (Perry et al., 2018). For scleractinian corals, one of the most significant consequences of OA is the decrease in the concentration of carbonate ions (CO_2^{-3}) (Kleypas and Yates, 2009). Projections suggest that future rates of coral reef community dissolution may exceed rates of $CaCO_3$ production (calcification), with the majority of coral reefs unable to maintain positive net carbonate production globally by 2100 (i.e., net loss) (Cornwall et al., 2021; Silverman et al., 2009; Hoegh-Guldberg et al., 2007).

These global climate change pressures are causing shifts in the composition of coral reef species, and the urgent focus now is on identifying, quantifying and maintaining reef ecosystem function so that coral reefs can continue to persist and deliver ecosystem services into the future (Harborne et al., 2017). To do this it is necessary to characterize reef health in terms of metabolism which includes calcification but also fundamental processes such as photosynthesis and respiration (Madin et al., 2016; Carlot et al., 2022). Photosynthesis fixes CO_2 in organic materials, whereas the reverse reaction (dark respiration) releases it. In scleractinian corals with zooxanthellae, the precipitation of $CaCO_3$ through calcification is tightly coupled to photosynthetic fixation of CO_2 and on average tends to be three times higher in daylight conditions than in darkness (Gattuso et al., 1999). Calcification rates can increase further through feeding on phytoplankton and suspended particles (Houlbreque and Ferrier-Pages, 2009). Overall, the excess organic production in a coral reef community (i.e., the difference between gross primary production and dark respiration) acts as a CO_2 sink, while calcification acts as a source of CO_2 (Lewis, 1977; Kinsey, 1985). Most reef flats are sources of CO_2 to the

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88 atmosphere despite the drawdown of CO_2 during the day via photosynthetic processes. This is

89 due to their low net fixation of CO_2 and rather large release of CO_2 by precipitation of calcium

90 carbonate (Ware et al, 1992; Gattuso et al, 1993; Gattuso et al, 1995; Smith, 1995;

91 Frankignoulle et al, 1996; Gattuso et al, 1996b).

92

93 One notable exception to this is in algal-dominated reef communities, which are sinks for

94 atmospheric CO_2. They exhibit larger excess community production and/or a lower community

95 calcification, (e.g., Kayanne et al, 1995; Gattuso et al, 1996a; Gattuso et al, 1997). The

96 morphological diversity of reef algae provides food (Overholtzer and Motta, 1999), habitat and

97 shelter (Price et al., 2011) for a number of invertebrate and fish species, with productivity

98 sustaining higher trophic levels. Calcified macroalgae can also contribute significantly to the

99 deposition of carbonates (Nelson, 2009). In particular, species of the genus *Halimeda* are

100 widely distributed across tropical and subtropical environments, contribute significantly to reef

101 calcification and productivity rates because of their fast growth and rapid turnover rates

102 (Vroom et al., 2003, Smith et al., 2004, Nelson, 2009) compared to corals or coralline red algae

103 (CRA). Calcification rates of *Halimeda* make it a major contributor to $CaCO_3$ in reefs in the

104 Caribbean (Blair and Norris, 1988; Nelson, 2009), Tahiti and the Great Barrier Reef (Drew,

105 1983; Payri, 1988). In certain locations, precipitation of calcium carbonate can approach 2.9

106 kg $CaCO_3$ m^{-2} yr^{-1}, positioning *Halimeda* as a major contributor to carbonate budgets within

107 shallow waters around the globe (Price et al., 2011). This group further occupies a diverse

108 range of environments (mangroves, seagrass beds, and coral reefs) and can produce structurally

109 complex mounds that serve as critical habitat for a diversity of important marine life (Rees et

110 al., 2007).

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Here, we compare metabolic and calcification rates of the dominant intertidal taxa of coral and macroalgae at Browse Island, a small island in the Kimberley bioregion located in the northern part of Western Australia. Unlike Southwestern Australia, which has one of the fastest increasing rates of change from cumulative human impacts (Halpern et al., 2019), the Kimberley represents one of the few "very low impact" tropical coast and shelf areas globally – only 3.7% of the global oceans fall in this category (Halpern et al., 2008). Few process studies have been carried out in the region due to the remoteness of these reef habitats, some of which are located 100s of km from the coastline, meaning that fieldwork and data acquisition can be difficult and costly. Rates of metabolism and calcification were determined in on-ship incubations in October 2016, April 2017 and October 2017. Using the proportional cover of the dominant benthic community, these rates were upscaled to gain whole of community metabolism estimates for the Browse Island habitats and provide new insights into reef ecosystem health and functioning in the absence of localised land- and sea-based anthropogenic variables (Harley et al., 2006; 157 Schindler, 2006; Walther, 2010).

2. Methods

2.1 Study site

Browse Island is located on the mid-shelf just inside the 200 m isobath off the Kimberley coast in northern Western Australia (14°6'S, 123°32'E; Fig. 1). The island is surrounded by a small (~ 4.5 km^2) planar platform reef consisting of a shallow lagoon, an extensive reef flat that is conspicuously absent to the northeast of the island, and a well-defined reef crest and slope. Tides are semidiurnal with a maximum range of < 5 m, exposing the reef crest and reef platform habitats during low tides. The intertidal habitats are characterised by low species richness and dominated by small turfing algae and calcified macroalgae of the genus *Halimeda* (15–22% and 6–9% cover respectively)) (Olsen et al., 2017). Coral assemblages are well developed with

303 cover of 5–8% in the intertidal habitats and 18% on the shallow reef slope (< 10 m) (Olsen et

304 al., 2017).

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306 *2.2 Algae and coral collection*

307 Specimens of the dominant coral and algal taxa were collected from the reef platform by hand

308 during low tide, immediately brought back to the vessel and kept in a holding tank with

309 circulating seawater. Macroalgae included the calcifying green alga *Halimeda opuntia*, which

310 was the dominant species of *Halimeda* on the reef platform, the green alga *Caulerpa* sp., and

311 the calcifying red alga *Galaxaura* sp. Pieces of turf algae (turf) as well as turf attached to a

312 piece of rock (turf + substrate) were measured. In April 2016, drift algae of the genus

313 *Sargassum* found floating on the water surface were also included although this taxa was not

314 been found growing anywhere on the reef. Hermatypic corals included *Pocillopora* sp.,

315 *Goniastrea* sp., *Porites* sp., *Heliopora* sp., *Acropora* sp. and *Seriatopora* sp. Whole pieces of

316 coral small enough to fit inside the incubation cores (inner diameter ~90 mm) were collected

317 to minimise tissue damage. All coral samples were > 50 mm diameter and therefore

318 operationally defined as adults and estimated to be at least 2 to 7 years old depending on the

319 taxa (Trapon et al., 2013).

320

321 *2.3 Light and dark incubations*

322 Light and dark incubations were undertaken on the back deck of the research vessel. Four 60

323 L holding tanks were placed in a shade-free spot under natural light conditions, filled with

324 seawater and connected to a flow-through seawater system driven by an Ozito PSDW-350 watt

325 Dirty Water Submersible Water Pump with a maximum flow rate of 7,000 litres/hour, which

326 ensured the setup remained at ambient temperature (Fig. 2). The intensity of photosynthetically

327 active radiation (PAR) was recorded for each set of incubations with a HOBO Micro Station

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328 logger (H21-002, Onset) placed inside one of the tanks. Six 1.56 L clear Perspex incubation

329 cores (24 total per incubation) fitted with stirring caps, were placed in each holding tank and

330 spaced evenly apart to minimise shading (Fig. 2).

331

332 Depending upon abundance, individual specimens of algae and coral were placed in 6 to 12

333 replicate incubation cores per taxa except where not enough individuals could be found. Table

334 1 shows the taxa incubated during each sampling trip and the number of replicates. Water

335 samples from the holding tanks were measured at each time point as controls and, in addition,

336 in October 2017, a separate seawater control (six replicate incubation cores with seawater) was

337 included. After a period of acclimation (1 to2 h), incubations were run over a four-hour period.

338 The light incubations were conducted while the sun was at its zenith providing full irradiance

339 to the samples. After two hours, the tubs were covered with a black lid ensuring no light could

340 enter and the samples incubated for two hours in the dark.

341

342 To estimate oxygen production or consumption during the incubations, a 40 mL water sample

343 was extracted from each of the 24 cores and the four tubs at the start of the incubations and

344 hourly thereafter. A port in the cap of each core allowed for sample collection using a syringe.

345 As the sample was removed, the same volume of liquid was automatically replaced from the

346 flowthrough tank into the core so that the core volume remained constant through the

347 experiment. Samples were immediately analysed for temperature and dissolved oxygen (O_2)

348 with a YSI 5100 bench-top oxygen and temperature meter with YSI 5010 BOD stirring probe,

349 calibrated daily in air. Sample pH was determined using a TPS Aqua pH meter with an Ionode

350 probe, calibrated daily with pH 7.00 and 10.00 buffers. A second 35 mL water sample was

351 collected from each core and tub and split between one 10 mL glass vacutainer for alkalinity

352 and duplicate 10 mL sterile vials for nutrient analyses. Nutrient samples were immediately

8

353   frozen and alkalinity samples were stored cool and dark. At the end of the incubation, algal and

354   coral specimens were frozen. All samples were transported to Perth, Western Australia, to be

355   analysed.

356

357   *2.4 Surface areas of coral and algal specimens*

358   Metabolic measurements were standardised by surface area of the incubated specimens since

359   this represents the area available for photosynthesis and nutrient uptake. The surface area of

360   specimens of coral, *Halimeda* and turf + substrate were estimated using a single wax dipping

361   method (Veal et al., 2010). Specimens were dried, weighed and then dipped in paraffin wax at

362   65°C. The waxed samples were weighed again, and the weight of the wax calculated. The

363   surface area was estimated from the wax weights against a calibration curve constructed by

364   wax dipping geometric wooden objects of known size. The surface areas of the remaining taxa,

365   were estimated from photographs in ImageJ (Rueden et al., 2017). The 'footprint' of each

366   sample, i.e. the surface area of reef occupied by the organism, was also estimated by tracing

367   the outline of the specimen photographed from straight above in ImageJ.

368

369   *2.5 Chemical analyses*

370   Concentrations of nitrate + nitrite (hereafter referred to as nitrate), ammonium, phosphate and

371   dissolved silica in water samples were analysed in duplicate by flow injection analysis (Lachat

372   QuickChem 8000) with detection by absorbance at specific wavelengths for silica [QuikChem

373   Method 31-114-27-1-D], nitrate [Quikchem Method 31-107-04-1-A] and phosphate

374   [QuikChem Method 31-115-01-1-G]), and by fluorescence for ammonia according to Watson

375   et al. 2005. Detection limits were 0.02 μmol L^{-1} for all inorganic nutrient species, with a

376   standard error of $< 0.7\%$.

377

378 From SOP3b in Dickson et al. 2007, total alkalinity was determined for single replicates to the

379 nearest 5 μmol L^{-1} equivalent (hereafter referred to as μmol L^{-1}) using an open cell Metrohm

380 titrator (841 Titrando, Burette: 800 Dosino 10 mL) with a Metrohm micro-glass pH probe

381 calibrated with Certipur buffer solutions at pH 2.00, 4.01, 7.00, and 10.00 (at 25.0°C). Samples

382 were kept in a Jubalo F12 temperature control water bath prior to decanting a 10 mL aliquot of

383 sample into a vessel with a water jacket maintaining temperature at 25.0°C. Samples were

384 titrated with 0.012 N HCl, standardised against sodium carbonate (99.95 to100.05 wt%) with

385 an initial volume of titrant added to reach pH 3.5. Titrations were run to an end-point of pH 3

386 with Gran plot (Excel macro) to determine the total alkalinity endpoint near pH 4.2. Carbonate

387 system parameters were calculated from pH (measured during the incubations) and total

388 alkalinity using the package 'seacarb' (Gattuso et al., 2018) in R (R Core Team, 2018).

389 Alkalinity and carbonate parameters were not determined in April 2016.

390

391 *2.6 Oxygen fluxes and calcification rate calculations*

392 The changes in O_2 concentrations during light- and dark incubations were expressed as mmol

393 per day assuming stable hourly production rates over 24 h. Any replicates where O_2 did not

394 increase during both of the light intervals or did not decrease during both of the dark intervals

395 were excluded from further analysis. Net fluxes of O_2 per day (mmol $day^{-1} m^{-2}$) were calculated

396 for each sample assuming a 12 h photoperiod. Calcification rates of corals and calcifying algae

397 (*Halimeda opuntia*. and *Galaxaura* sp.) were estimated using the alkalinity anomaly method

398 (Smith and Key, 1975) uncorrected for changes in nutrient concentration (Chisholm and

399 Gattuso, 1991) where precipitation of one mole of $CaCO_3$ leads to the reduction of total

400 alkalinity by two molar equivalents. Rates per surface area (mmol $day^{-1} m^{-2}$) were obtained by

401 dividing these values by the surface area of each specimen.

402

403　A census-based approach was used to estimate the amount of $CaCO_3$ and O_2 produced by a

404　single taxon per unit area of reef surface per year (Shaw et al., 2016). The rates of calcification

405　and net O_2 production per day were divided by the 'footprint' area of each specimen. To

406　estimate the relative contributions from each taxon to community production per m^2 of reef,

407　these rates were multiplied by the relative percent cover in each of the major habitats. Estimates

408　of percent cover based on drop camera image analysis were obtained from Olsen et al. (2017).

409　The productivity rates for individual coral species were combined into one value for coral.

410

411　*2.7 Statistical analyses*

412　The relationships between net changes in pH and O_2 and between net O_2 production and net

413　calcification (in light and dark incubations) were examined by linear regression. Significance

414　of regressions were calculated for algae, calcified algae and corals and the 95% confidence

415　intervals for the slope of each line in R (R Core Team, 2018). Regressions were examined with

416　ANOVA and deemed significant if $p < 0.05$.

417

418　**3　Results**

419　*3.1 Experimental conditions*

420　Nutrient concentrations were low and similar among sampling trips (Table 2), as is

421　characteristic of tropical Eastern Indian Ocean offshore waters (McLaughlin et al., 2019).

422　Concentrations of nitrate were 0.05 to 0.17 μmol L^{-1}, ammonium 0.12 to 0.13 μmol L^{-1},

423　phosphate 0.07to 0.1 μmol L^{-1}, and silicate 2.3 to 3 μmol L^{-1}. Oxygen was around 0.19 mmol

424　L^{-1} to 0.22 mmol L^{-1} and salinity 34.2 to 34.8 ppt. Light and temperature conditions in the

425　incubations were representative of *in situ* conditions on the reef platform and were similar

426　among trips. PAR levels were 1500 to 1587 μE m^{-2} s^{-1} and slightly higher in October.

427　Temperatures were 28.3 to 32.8°C and highest in April. Carbonate system parameters were

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430   not obtained for April 2016 due to instrument error, and some minor differences in pCO2,

431   HCO_3^-, CO_3^-, DIC and Ω Aragonite were noted between October 2016 and 2017 (Table 2).

432   Alkalinity and pH were both higher in 2016, and there were associated minor differences in

433   the concentrations of the carbonate species and the aragonite saturation state (Table 2).

434

435   *3.2 Changes in oxygen and pH*

436   Changes in dissolved O_2 differed among taxa, and between light and dark incubations. In the

437   seawater controls O_2 changed by < 0.01 mmol h^{-1} in both light and dark incubations, showing

438   that the contribution of any organisms in the seawater itself to O_2 production and dark

439   respiration was minimal. No corrections were therefore applied. In the light incubations O_2

440   productivity fluxes were positive for all taxa (Fig. 3, top panel). The highest light flux of O_2

441   of ~380 mmol m^{-2} day^{-1} was measured for *Galaxaura* in October 2017 (Fig. 3, top). Corals

442   generally produced 100 to 260 mmol O_2 m^{-2} day^{-1} in the light, except *Heliopora,* which had

443   a flux of 50 to 80 mmol O_2 m^{-2} day^{-1}. All taxa consumed O_2 during the dark incubations

444   when changes in O_2 are due to dark respiration, with mean fluxes of -15 to -190 mmol O_2

445   m^{-2} day^{-1} (Fig. 3, middle). All algae were net autotrophic and produced 6 to 111 mmol O_2

446   m^{-2} day^{-1} with the highest net O_2 flux measured for *Galaxaura* and turf at 111 and 36 mmol

447   O_2 m^{-2} day^{-1} respectively (Fig. 3, bottom). In contrast, around half of the corals were net

448   consumers of O_2 and average net fluxes spanned a wide range from -42 to 47 mmol O_2 m^{-2}

449   day^{-1}.

450

451   In the light incubations, pH generally increased by 0.03 to 0.25 h^{-1} for all taxa, except for

452   *Halimeda* in April 2016 and October 2017, which showed no change or a very small increase

453   (Fig. 4, top panel). In dark incubations, mean pH decreased for all taxa by 0.02 to 0.21 h^{-1}

454   indicative of a net increase in CO_2 through dark respiration (Fig. 4, middle). Non-calcifying

455　algae (*Sargassum*, *Caulerpa* and turf) raised net pH by 0.02 to 0.05 h^{-1} (assuming equal

456　periods of light and darkness) (Fig. 4, bottom panel). The net change in pH was generally

457　negative for corals and calcifying algae (-0.01 to -0.08 h^{-1}), except for the coral *Goniastrea*

458　in April and October 2016 (0.01 h^{-1}) and the calcifying alga *Galaxaura* (0.03 h^{-1}; Fig. 3,

459　bottom).

460

461　Net changes in pH are largely driven by metabolic uptake and release of CO_2. We found

462　positive relationships between changes in pH and net production or consumption of O_2 except

463　in seawater controls where changes in O_2 and pH were minor (Fig. 5). The relationships for

464　algae, calcifying algae and coral were all significant, but had relatively low adjusted r^2 values

465　of 0.59, 0.46 and 0.19 respectively, suggesting significant variability among species and

466　individuals within each of these groups.

467

468　*3.3 Calcification Rates*

469　Corals, *Halimeda* and *Galaxaura* had positive calcification rates in light ranging from 4.2 to

470　18.4 g $CaCO_3$ m^{-2} d^{-1} (Fig. 6, top panel). In the dark, calcifying rates were smaller and just

471　under half of the rates were negative suggesting dissolution of $CaCO_3$ (Fig. 6, middle panel).

472　The resulting net calcification rates (based on equal periods of light and dark - monthly

473　average sunrise and sunset at Browse Island of 0552 and 1739 for April, and 0519 and 1754

474　for October; WillyWeather, 2022) were all positive and ranged from 1.9 to 9.9 g $CaCO_3$ m^{-2}

475　d^{-1} (Fig. 6, bottom). Rates of calcification were strongly linearly correlated to net O_2

476　production and were significantly higher in light than in darkness for both corals and algae

477　(Fig. 7).

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479　*3.4 Contributions to community production*

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481   In intertidal habitats (lagoon and high reef platform) around Browse Island, the estimated

482   relative contributions of coral (8 % cover) and *Halimeda* (7 % cover) to the reef production

483   of $CaCO_3$ were similar, around 600 to 840 g m^{-2} year^{-1} (Fig. 8, top panel). The low reef

484   platform had very low coral cover of < 3% (Fig. 8, middle), which therefore made a smaller

485   contribution to calcification of ~240 g $CaCO_3$ m^{-2} year^{-1} in this habitat (Fig. 8, top). In

486   contrast, calcification on the subtidal reef slope was predominantly from corals (19 % cover),

487   which produced ~1540 g $CaCO_3$ m^{-2} year^{-1}, around twice the amount compared to *Halimeda*

488   (7 % cover). *Galaxaura*, which had high measured rates of productivity and calcification, was

489   extremely rare (0.02 % total cover found only in October 2017; Olsen et al., 2017) and thus

490   its contribution to community calcification and productivity were negligible. Turf was

491   responsible for the majority of the O_2 production in all habitats and produced an estimated 8

492   to 13 mmol O_2 m^{-2} d^{-1} compared to < 2 for *Halimeda* mmol O_2 m^{-2} d^{-1} and −4 to −1 mmol O_2

493   m^{-2} d^{-1} for corals (Fig. 8, second panel from top).

494

495   4   **Discussion**

496   Mesocosm experiments have shown that reef-building (hermatypic) corals tend to reduce pH

497   and consume O_2 (e.g. (Gattuso *et al.* 2015; Smith *et al.* 2013)), whereas calcifying macroalgae

498   increase pH and O_2 during daytime (Borowitzka and Larkum 1987; Smith *et al.* 2013). Both

499   corals and calcifying macroalgae reduce pH and O_2 concentrations due to respiration during

500   nighttime, but the rates of change differ among species (Smith *et al.* 2013). The organisms

501   investigated in the present study showed typical patterns of O_2 production in daylight and

502   consumption in darkness to other similar island reef systems as a result of photosynthesis and

503   dark respiration, but the metabolic measurements showed clear differences among taxonomic

504   groups. Algae had higher positive net O_2 fluxes with rates of 18 to 350 µmol O_2 m^{-2} day^{-1}, of

505   which the red calcifying alga *Galaxaura* sp. had the highest rate of net productivity by far. For

Deleted: This study investigated the metabolism of coral and algae on the reef of remote Browse Island, found on the mid-shelf region of the Kimberley in Western Australia. Due to its remoteness, Browse Island presented a unique opportunity to observe these organisms in a pristine habitat where direct anthropogenic pressures are minimal. The Island has semidiurnal tides reaching a maximum range of 5 m (Olsen et al., 2017), half the magnitude of tides experienced by reefs closer to the coast (McLaughlin et al., 2019), and its benthic structure is very different from both Kimberley inner and outer shelf reefs. Lowe et al. (2015) have revealed that strongly tide-dominated circulation can occur on Kimberley reef platforms and the trapping of water on a reef, such as that found at Browse Island, can provide benefits for reef organisms in terms of avoiding aerial exposure. However, it can dramatically increase the residence (or flushing) times of reefs, which can lead to extreme diel variations in water quality (Lowe et al., 2015). Seawater O_2 and carbonate chemistry can vary over diel tidal cycles, like those found at Browse Island, and are related to patterns in autotrophic photosynthesis and dark respiration (e.g., Duarte et al., 2013). Primary production and the uptake of CO_2 by coral and algae during daylight hours results in elevated pH and an elevated aragonite saturation state (Ω_{arag}) during the day when calcification rates peak. The process of calcification decreases pH in the surrounding water, but for calcifying autotrophs CO_2 uptake and fixation through photosynthesis can potentially offset changes to the carbonate chemistry caused by calcification (Anthony et al., 2011; Smith et al., 2013). ¶
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corals, the relatively high O_2 increase measured in daylight was coupled with high rates of respiration in darkness, creating a negligible or negative net O_2 production for most species, except *Porites* sp. in April 2016 and *Seriatopora* sp. in October 2016 and 2017 which were net positive. Although autotrophic, our data indicates that the majority of the corals we studied utilise heterotrophic supply through feeding to help sustain growth in addition to photosynthesis by zooxanthellae (Houlbreque and Ferrier-Pages, 2009). These patterns are generally in agreement with those reported elsewhere. For example, fleshy and calcifying algae showed net diel O_2 production, whereas corals generally consumed O_2, i.e. were net heterotrophic, on islands in the South Pacific (*Porites* sp.) and the Caribbean (*Madracis* sp.) (Smith et al., 2013).

Concurrent with changes in O_2 were changes in seawater pH, where pH increased in daylight (except for *Halimeda* in April 2016 where no change was measured) and decreased in darkness. The effects of metabolic activity on bulk pH (uptake and release of CO_2 through photosynthesis and dark respiration) cannot be directly separated from that of calcification, which is associated with the release of H^+ ions thereby decreasing pH (Jokiel, 2011). However, differences were observed in the net pH change in incubations between calcifiers and non-calcifiers. The net effect of non-calcifiers on seawater pH was positive while the majority of calcifiers caused net pH to decline. In the present study, *Halimeda* (April 2016) and *Goniastrea* (April and October 2016) caused relatively minor increases in pH, whereas the calcifying alga *Galaxaura* elevated pH by, on average, 0.03 units, comparable to the net effect of non-calcifiers. This is not surprising given the high rate of O_2 production measured for *Galaxaura*, which is associated with sufficient levels of CO_2 fixation to compensate for the reduction in pH associated with calcification in this species. A strong link was observed between metabolism and pH in all taxa, demonstrated as linear relationships between changes in pH and O_2 during the incubations.

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561 Previous research by Smith et al. (2013) identified two broad patterns: metabolic changes in

562 O_2 in non-calcifiers (fleshy and turf algae) linked to large changes in pH (steep slopes), and

563 metabolic changes in O_2 in calcifying organisms (*Porites* sp. *Madracis* sp. and *Halimeda* sp.)

564 producing little or no change in pH (shallow slopes). This is contrary to the present study's

565 observations where pH and O_2 relationship gradients were similar for calcifiers and non-

566 calcifiers. Non-calcifying organisms were found to consistently have a net positive effect on

567 both pH and O_2. Change in pH for the same net change in O_2 was elevated for non-calcifiers

568 compared to calcifiers.

569

570 Production and accumulation of reef framework carbonate is controlled by the relative rates of,

571 and the interactions between, a range of ecologically, physically and chemically driven

572 production and erosion processes (Perry et al., 2008; Montaggioni and Braithwaite, 2009), with

573 the relative importance of different taxa for $CaCO_3$ production differing among reefs and

574 among habitats within reefs. Coral growth can be measured in several ways: linear extension

575 rate, global skeletal growth and calcification rate (measured using the alkalinity technique or

576 by ^{45}Ca incorporation) (Houlbreque and Ferrier-Pages, 2009). Methods to calculate

577 calcification can vary in accuracy. Overestimates of calcification rates can result from

578 calculations based on changes in alkalinity, while those relying on $CaCO_3$ content and growth

579 measurements (either through staining or tagging segments), may produce minimum estimates

580 as loss of new tissue is not accounted for (Hart and Kench, 2007; Houlbreque and Ferrier-

581 Pages, 2009). The alkalinity method employed in the present study was the best possible option

582 when working in a remote location where actual growth rates cannot be easily assessed, or use

583 of radioisotopes was limited. Rates of net community calcification for reef flats worldwide

584 range from 7.3 to 90 mol (730 to 9000 g) $CaCO_3$ m^{-2} $year^{-1}$ with an average of 47 mol (4700

585 g) $CaCO_3$ m^{-2} $year^{-1}$ (Atkinson, 2011). The patterns found in the present study — higher

16

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589   calcification rates in daylight compared to in darkness for all corals and calcifying algae — are

590   typical. However, the coral $CaCO_3$ production rates per reef area (7 to 8% cover low reef

591   platform, 19% reef slope) measured here (240 g m^{-2} year^{-1} for low reef platform, 610 to 756 g

592   m^{-2} year^{-1} in the other intertidal habitats, and 1536 g m^{-2} year^{-1} on the reef slope) were

593   somewhat lower than values reported elsewhere. In 2016, the dark rates of calcification in

594   corals were less than 50% of the rates in light with some (*Porites* and *Heliopora)* negative.

595   Dark rates of calcification in 2017 were negative or near zero for all species except *Porites,*

596   *Pocillopora* and *Seriatopora*. Houlbreque et al. (2004) showed that coral feeding enhances dark

597   calcification rates in scleractinian corals, but incubations in our study were done in absence of

598   supplemental feeding. The trend observed here may be due to some dissolution of $CaCO_3$ due

599   to the reduced pH during dark incubations or could be an artefact of the experimental

600   conditions. This result should therefore be taken with some caution, in particular for *Porites* in

601   October 2016, which saw the largest decrease (Fig. 5, middle panel). However, the resulting

602   strong relationship between net carbonate production and net carbonate consumption is

603   consistent with previous studies both *in situ* and in mesocosms (Albright et al., 2013).

604

605   Corals are typically the primary framework-producing components on a tropical reef and

606   dominate carbonate production per unit area (Vecsei, 2004), however additional $CaCO_3$ is

607   produced by calcareous crustose coralline algae (CCA) and calcareous algae of the genus

608   *Halimeda*, (e.g. Payri, 1988). Sprawling lithophytic species of *Halimeda*, like the majority of

609   the *Halimeda* around Browse Island, tend to be fast growing and have high calcification rates

610   (Hart and Kench, 2007). Rates of calcification per area of 100% *Halimeda* cover have been

611   estimated to 400 to 1667 g $CaCO_3$ m^{-2} year^{-1} (in Hart and Kench, 2007 Suppl info). In other

612   locations, *Halimeda* has been estimated to contribute around 1100 to 2400 g $CaCO_3$ m^{-2} year^{-1}

613   to benthic carbonate production (Drew, 1983; Freile et al., 1995; Hudson, 1985; Kangwe et al.,

614   2012; Payri, 1988; Rees et al., 2007), which is higher than the 600 to 840 g $CaCO_3\,m^{-2}\,year^{-1}$

615   estimated for *Halimeda opuntia* in the intertidal habitats in the present study. These rates

616   depend both on the intrinsic calcification rates and on the abundance or cover of algae (6.1 to

617   8.7% cover on Browse, which corresponds to ~150 to 250 g dw m^{-2}).

618

619   Nutrient capacity is one important driver of productivity in many reef ecosystems. The rate at

620   which nutrients are recycled between the constituents of the system (the ambient nutrient

621   availability, and the nutrients stored within plant and animal biomass) depends on input from

622   a variety of sources (e.g., associated with seasonal rains or upwelling) (DeAngelis, 1992;

623   Hatcher, 1990). Coral reefs, typically have low ambient nutrient availability and receive little

624   sustained exogenous nutrient input (Hatcher, 1990; Szmant, 2002), thus the high rates of

625   production found within these ecosystems are largely attributed to the nutrients stored and

626   cycled by living biomass (Pomeroy, 1974; DeAngelis et al., 1989; Sorokin, 1995). Fishes

627   typically make up a substantial component of living biomass on coral reefs and represent an

628   important reservoir of nutrients in these ecosystems (Allgeier et al., 2014). Contrary to our

629   expectations given its remote location in an area of apparently low anthropogenic impacts, the

630   reef platform around Browse Island was depauperate with a conspicuous lack of diversity in

631   key groups including macroalgae, macroinvertebrates and teleost browsers (Bessey et al.,

632   2020). McLaughlin et al. (2019) found surface water standing stock nutrient concentrations

633   low along Kimberley shelf. Conditions at Browse Island were similar with low water column

634   nutrients for nitrate, ammonia and phosphate during all trips. Understanding how changes in

635   animal populations alter nutrient dynamics on large ecological scales is a relatively recent

636   endeavour (Doughty et al., 2015). Allgeier et al. (2016) showed that targeted fishing of higher

637   trophic levels reduces the capacity of coral reef fish communities to store and recycle nutrients

638   by nearly half. Fish-mediated nutrients enhance coral growth (Meyer et al., 1983) and primary

639 production (Allgeier et al., 2013), and may regulate nutrient ratios at the ecosystem scale

640 (Allgeier et al., 2014).

641

642 The Kimberley region-wide averages of coral cover and macroalgal cover are 23.8% and 7.1%

643 (Richards et al., 2015) respectively. However, this relationship at Browse Island is reversed,

644 with macroalgae more dominant at 28% total cover to that of coral at 9% total cover. On the

645 Browse Island reef platform, the same pattern is observed where averages were 5 to 8% for

646 coral and 32% for macroalgae, differing from those of the regional averages of 14.4% and

647 15.5% of coral and macroalgae respectively (Richards et al., 2015). While the estimates

648 provided here approximate the relative contributions of *Halimeda* and coral to $CaCO_3$

649 production, they do not add up to a whole system budget. There are other organisms likely to

650 contribute significantly. For example, the present study did not measure metabolic or

651 calcification rates of encrusting coralline algae, which, although making up a modest 1.0 to

652 3.0% of the benthic cover in the lagoon and reef platform habitats at Browse Island, become

653 more prominent at 11.8 to 14.1% on the reef crest and slope (Olsen, unpublished data). To

654 calculate the true $CaCO_3$ production per area of reef, the calcification rate would need to be

655 multiplied by the benthic cover of coralline algae and the square of the benthic rugosity (Eakin,

656 1996). Using typical values for rugosity from Eakin (1996) of 1 to 1.4 for the lagoon and reef

657 platform and 1.7–2 for the reef crest and slope, and assuming a typical calcification rate of

658 1500 to 2500 g m^{-2} $year^{-1}$ (for 100% flat-surface cover) (Hart and Kench, 2007), the

659 contribution of encrusting coralline algae to calcification in the lagoon and reef platform would

660 be minor at 70 to 134 g $CaCO_3$ m^{-2} $year^{-1}$. However, they could produce a significant amount

661 of 980 to 1360 g $CaCO_3$ m^{-2} $year^{-1}$ on the reef crest and slope, which is somewhere in between

662 the production rates estimated for *Halimeda* and corals. Encrusting coralline algae may

663 therefore contribute significantly to the $CaCO_3$ budget at Browse Island, at least in deeper

664   habitats. These values are similar to those measured elsewhere, for example 870 to 3770 g

665   $CaCO_3$ m^{-2} year^{-1} at Uva reef in the eastern Pacific (Eakin, 1996).

666

667   Metabolic rates of primary producers are clearly influenced by a multitude of factors including

668   hydrodynamics, irradiance, and nutrient availability (Smith et al., 2013). We were able to detect

669   considerable diurnal changes in water chemistry due to metabolic rates, since our experiments

670   were conducted in small enclosed mesocosms. The effect of metabolism on water chemistry is

671   expected to dissipate downstream in a more turbulent or dynamic environment (Anthony et al.

672   2011). However, coral and algae metabolic rates and resultant flux from diffusive boundary

673   layer also increases with flow rates (Carpenter et al. 1991; Lesser et al. 1994; Bruno and

674   Edmunds 1998; Mass et al. 2010). Because our experiments were conducted in near no-flow

675   chambers (mesocosm water was replenished with fresh seawater in small amounts during

676   sample extraction), our measurements are conservative values and likely represent the lower

677   range of potential effects that these reef organisms have on surrounding water chemistry,

678   however where residence times can be extended, particularly when trapping of water on the

679   reef at low tides occurs, our results are likely reflective of how these benthic organisms affect

680   water chemistry in the lagoonal habitats of Browse Island.

681

682   **5   Conclusions**

683   This study investigated the metabolism of coral and algae on the reef of remote Browse

684   Island, found on the mid-shelf region of the Kimberley in Western Australia. Due to its

685   remoteness, Browse Island presented a unique opportunity to observe these organisms in a

686   pristine habitat where direct anthropogenic pressures are minimal. Browse Island is the only

687   emergent mid-shelf reef in the Kimberley bioregion having semidiurnal tides reaching a

688   maximum range of 5 m (Olsen et al., 2017), half the magnitude of tides experienced by reefs

20

689 closer to the coast (McLaughlin et al., 2019). Its benthic structure is very different from both

690 Kimberley inner (e.g. Montgomery Reef, Adele and Cassini Islands) and outer (e.g. Ashmore

691 Reef and Rowley Shoals) shelf reefs. The relative contributions of algae and corals to reef

692 productivity are likely to differ across the Kimberley shelf, with corals becoming more

693 important in offshore waters and algal calcifiers being important on the mid-shelf. Estimated

694 aerial production rates did not take into account the relief (differences in height from place to

695 place on the reef surface) of the substrate. The reef platform surrounding Browse Island has

696 relatively low surface relief, whereas the reef slope and crest have high rugosity, which

697 means production rates in the latter environments may be underestimated. Despite these

698 limitations, the rates estimated in this study are similar to those measured elsewhere.

699

700 The higher cover of *Halimeda* and the low coral cover at Browse Island compared to other

701 reefs in the region mean that corals and *Halimeda* contribute equally to productivity rates of

702 $CaCO_3$ on the Browse Island reef flat, however, their relative contributions to the reef

703 framework and sedimentary budget of the reef is unknown. To gain an understanding of the

704 relationships between carbonate production and sinks on the reef, further study into the types

705 and amounts of $CaCO_3$ material found in each reef sink is necessary. The Kimberley coastal

706 shelf, which is characterised by coral reef environments with clear, low nutrient waters and

707 low productivity, has largely escaped land-based anthropogenic impacts, but has been

708 negatively affected by climate-driven coral bleaching and mortality, for example from heat

709 waves at Scott Reef in 1998 and 2016 (Smith et al., 2008, Gilmour et al., 2013 and Hughes et

710 al., 2017) and Ashmore Reef in 2003 and 2010 (Ceccarelli et al., 2011 and Heyward, 2011).

711

712 There is lack of sufficient observations of pCO2, nutrients and research on the upper ocean

713 carbon cycle from the Indian Ocean (Sreeush et al., 2020), and which are critical to modelling

Deleted: and is host to a different benthic community composition compared to the closest reefs both inshore (e.g. Montgomery Reef, Adele and Cassini Islands) and offshore (e.g. Ashmore Reef and Rowley Shoals).

718 of ocean acidification in the region (Panchang and Ambokar, 2021). The uptake of carbon

719 dioxide by the ocean alters the composition of seawater chemistry with elevated partial

720 pressures of carbon dioxide (pCO2) causing seawater pH and the $CaCO_3$ saturation state to

721 decrease (Feely et al, 2004). Ocean acidification directly threatens crucial trophic levels of

722 the marine ecosystem. Baseline reef measurements in undisturbed areas like Browse Island

723 are important to understand exclusively climate-driven stressors in lieu of local

724 anthropogenic pressures normally associated with coastal tropical reefs. The effects of

725 temperature stressors on reef communities and their productivity remain to be investigated in

726 this region. Different components of the reef around Browse Island are likely to have

727 different vulnerabilities to warming and heat waves. Future environmental stressors leading

728 to changes in benthic community composition, structure and subsequent changes in reef

729 productivity and in rates of production of $CaCO_3$, could have major implications for Browse

730 Island.

731

732 **Author contribution:** M. James McLaughlin – Conceptualization, formal analysis,

733 investigation, resources, methodology, visualisation, and writing (original draft preparation);

734 Cindy Bessey - Investigation, resources, project administration, and writing (review and

735 editing); Gary A. Kendrick - Conceptualization, funding acquisition, project administration,

736 supervision, and writing (review and editing); John Keesing - Conceptualization, funding

737 acquisition, investigation, resources, supervision, and writing (review and editing); Ylva S.

738 Olsen - Conceptualization, formal analysis, investigation, project administration, resources,

739 methodology, visualisation, and writing (original draft preparation)

740

Deleted: The effects of temperature stressors on reef communities and their productivity remain to be investigated in this region.

750 **Acknowledgements**

754 **Figures**
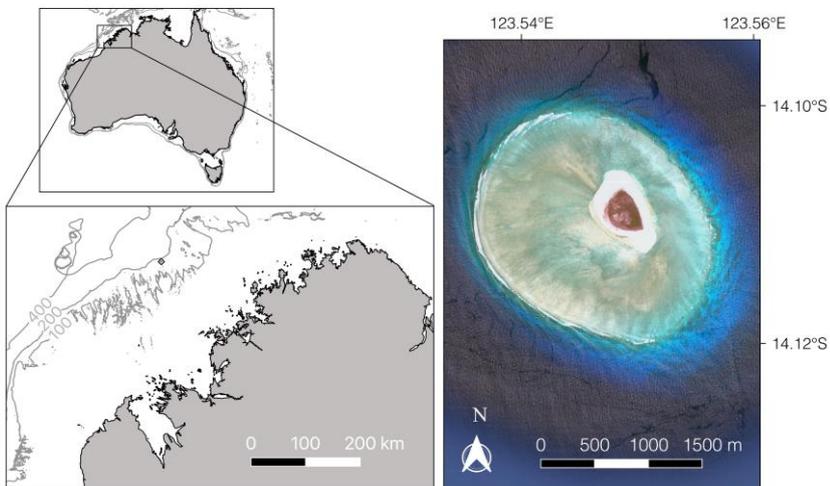
755

756 **Figure 1.** The study site, Browse Island (diamond, bottom left map), is located just inside the

757 200-m isobath on the continental shelf. The small map (top left) shows the location of the island

23

758   relative to the Australian coastline with the 100, 200 and 400 m isobaths marked in gray. The

759   satellite image (right; © Google Earth 2018) shows the extent of the reef.
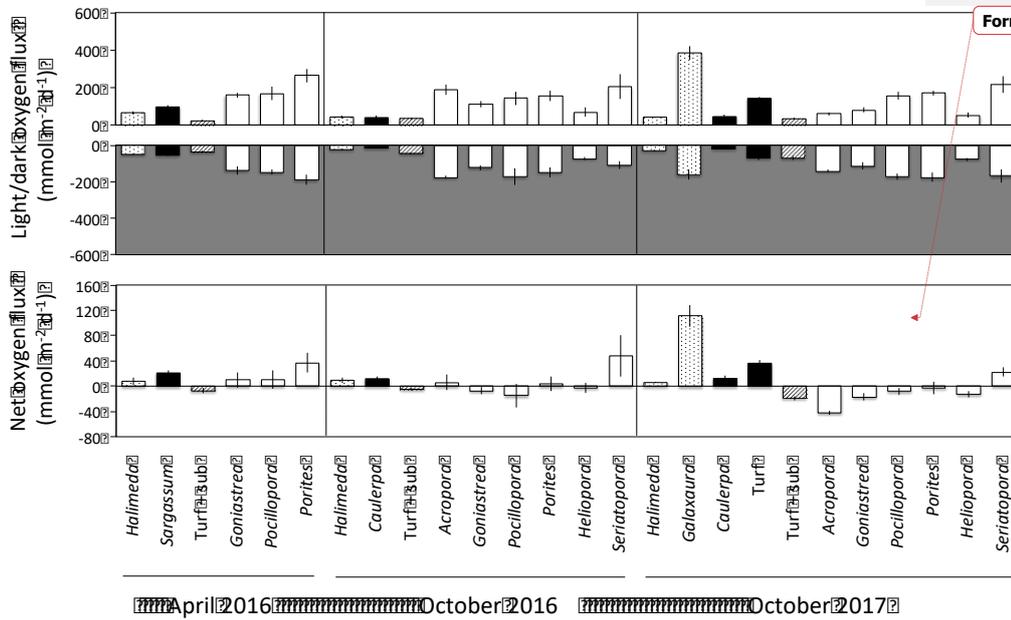
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Figure 2. Experimental setup of respirometry incubations for Browse Island coral and macroalgae.

762

763

Figure 3. Net changes in oxygen (means ± se) in light (top) and dark (middle) incubations of calcifying algae (stippled), macroalgae and turf (black), turf + substrate (diagonal stripes) and coral (white) standardised by specimen surface area. The bottom panel shows the net daily production of oxygen (means ± se) assuming a 12-h photoperiod and stable rates of photosynthesis and dark respiration over a 24-h period.

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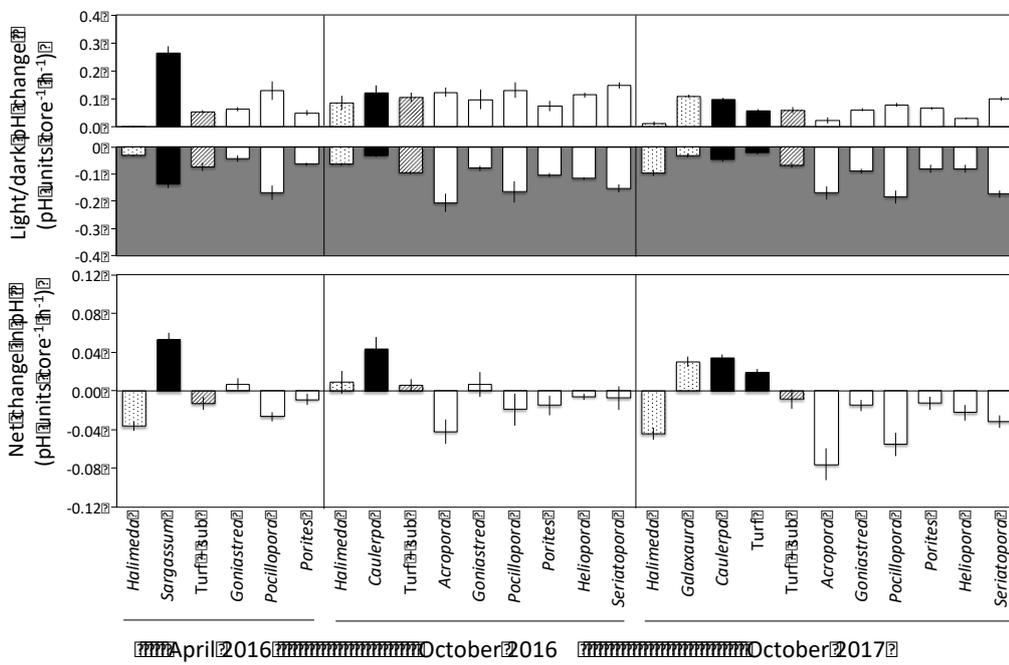
Figure 4. Net changes in pH per hour for each 1.56-L incubation core (means ± se) in light
(top) and dark (middle) incubations calcifying algae (stippled), macroalgae and turf (black),
turf + substrate (diagonal stripes) and coral (white). The bottom panel shows the net change in
pH per hour (means ± se) assuming equal periods of light and darkness.

775

Net change in pH (core^{-1} h^{-1})

Net change in O$_2$ (μmol core^{-1} h^{-1})
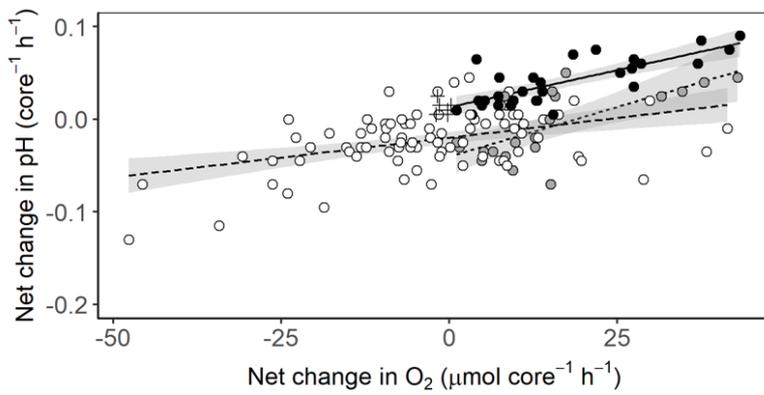
+ Control ——●—— Algae ····○···· Calcified algae --○-- Coral

776

Figure 5. Net change in pH versus O$_2$ per 1.56-L incubation core assuming equal periods of

light and darkness. Linear relationships are fitted with 95% confidence intervals shown in gray.

For algae; net change in pH = 0.13 + 0.0016 × net change in O$_2$ (ANOVA: $F_{1,27}$ = 41.15, p

<0.001). For calcified algae; net change in pH = −0.04 + 0.0021 × net change in O$_2$ (ANOVA:

$F_{1,19}$ = 17.86, p <0.001). For corals; net change in pH = −0.02 + 0.00086 × net change in O$_2$

(ANOVA: $F_{1,82}$ = 18.88, p <0.001).

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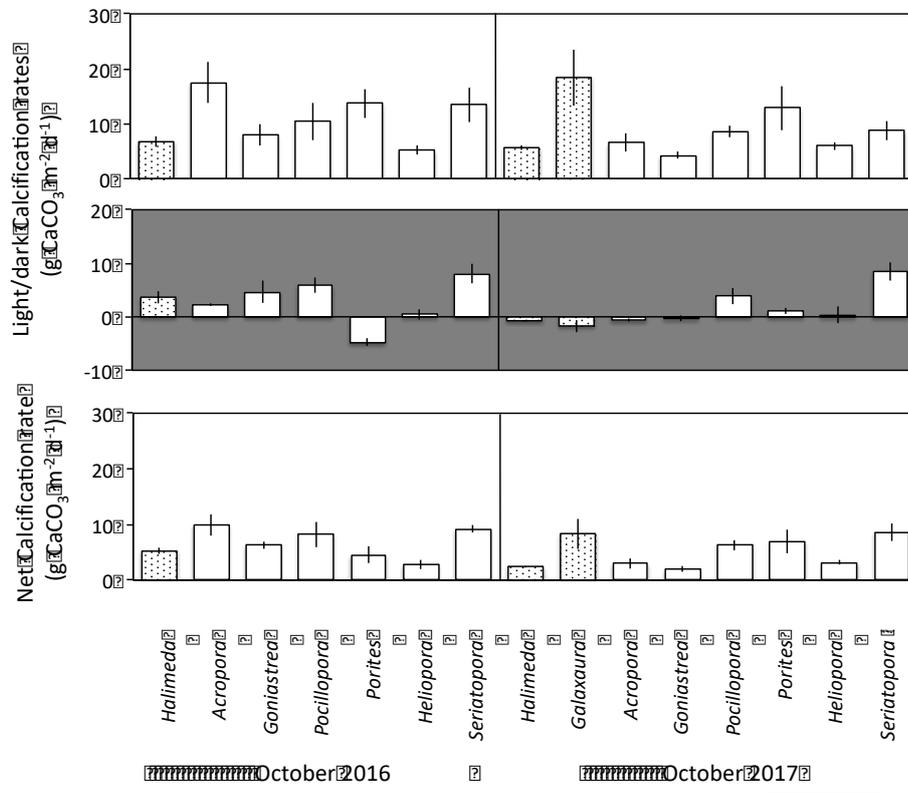
Figure 6. Calcification rates for corals (white) and calcifying algae (stippled) (means ± se) in

light (top) and dark (middle). The bottom panel shows the daily net calcification rate (means ±

se) assuming a 12-h photoperiod.

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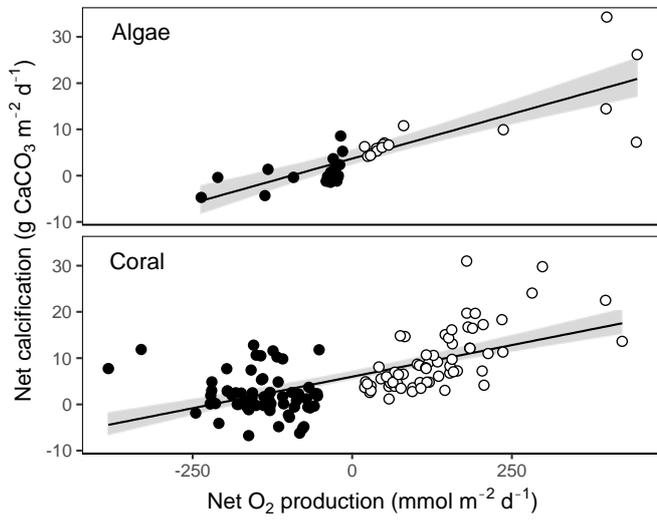
Figure 7. Relationship between net calcification rate and net productivity for calcifying algae
(top) and corals (bottom). Open circles indicate rates measured in light and closed circles rates
measured in dark. Linear fits are shown with 95% confidence intervals in gray. For calcified
algae; net calcification = 3.6 + 0.039 × net O_2 production (ANOVA: $F_{1,32}$ = 67.0, p <0.001).
For corals; net calcification = 5.99 + 0.027 × net O_2 production (ANOVA: $F_{1,126}$ = 82.2, p
<0.001).

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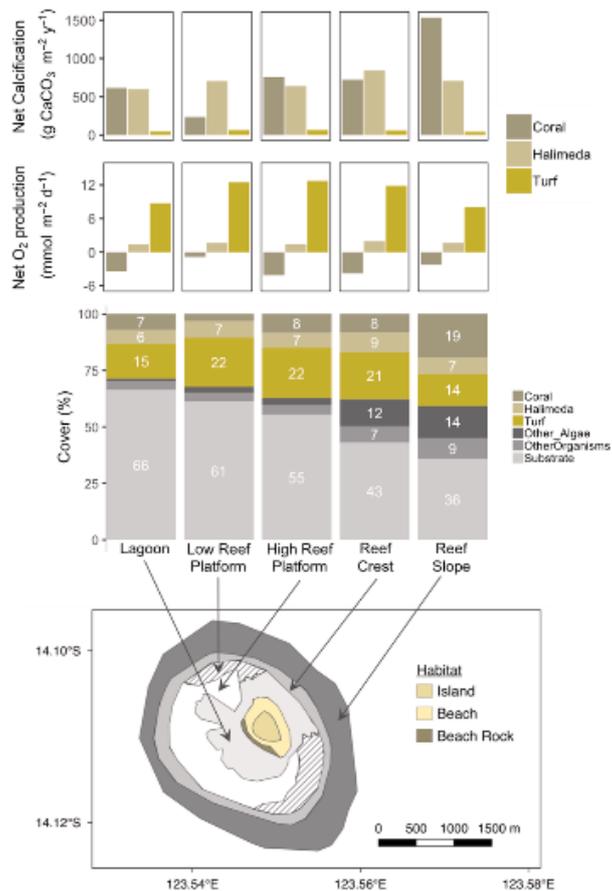
Figure 8. Map of the reef around Browse Island showing the major habitat types (bottom
panel). Reef surface percent cover of coral, *Halimeda*, turf and other categories in each habitat
(middle panel) based on drop-camera image analysis data from (Olsen *et al.* 2017). Net
calcification and net oxygen production by coral, *Halimeda* and turf per m^{-2} of reef (top two
panels) scaled up by multiplying rates obtained from incubations of each taxon by the percent
cover in each habitat.

31

804 **Tables**

805 **Table 1.** Taxa measured in on-ship incubation experiments including the number of replicate

806 specimens measured (one specimen per incubation core). Some of the specimens were not

807 included in the final analysis due to sampling errors or due to O_2 not increasing during both of

808 the light intervals or not decreasing during both of the dark intervals; the resulting number of

809 specimens used are shown in brackets.

	Taxa	Apr 2016	Oct 2016	Oct 2017
Algae	*Halimeda opuntia*	6 (5)	6	6
	Turf algae + substrate	6 (5)	6	6
	Turf algae	-	-	6
	Sargassum sp.	12	-	-
	Caulerpa sp.	-	6	6
	Galaxaura sp.	-	-	6 (5)
Coral	*Pocillopora* sp.	6	6	6
	Goniastrea sp.	6 (5)	6	6
	Porites sp.	5	6	6
	Heliopora sp.	-	6 (5)	6
	Acropora sp.	-	5	6
	Seriatopora sp.	-	4	6
	Seawater control	-	-	6

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812 **Table 2.** Ambient concentrations of parameters measured during incubations (means ± se);

813 nutrients ($NO_3^- + NO_2^-$ = nitrate + nitrite, NH_4^+ = ammonium, PO_4^{3-} = orthophosphate, Si =

814 silica) and oxygen (O_2), total alkalinity (TAlk), Photosynthetically Active Radiation (PAR),

815 temperature (T) and salinity. Calculated carbonate system parameters (means ± se); CO_2

816 partial pressure (pCO_2), concentrations of HCO_3^-, CO_3^{2-} and dissolved inorganic carbon

817 (DIC), and the saturation state of aragonite (Ω Aragonite). In April 2016, two replicate PAR

818 measurements were taken at 11:00, 12:00 and 13:00 h. In October 2016 and 2017, PAR was

819 measured every minute and values between 11:00 and 13:00 h averaged.

	Apr 2016	Oct 2016	Oct 2017
Number of replicates (n)	8	10	12
$NO_3^- + NO_2^-$ (µmol L^{-1})	0.15 ± 0.04	0.05 ± 0.01	0.17 ± 0.01
NH_4^+ (µmol L^{-1})	0.12 ± 0.02	0.13 ± 0.01	0.13 ± 0.01
PO_4^{3-} (µmol L^{-1})	0.08 ± 0.01	0.07 ± 0.00	0.09 ± 0.00
Si (µmol L^{-1})	2.74 ± 0.04	2.93 ± 0.04	2.30 ± 0.02
O_2 (µmol L^{-1})	19.3 ± 0.19	20.8 ± 0.16	23.4 ± 0.29
PAR 11–13 h (µE m^{-2} s^{-1})	1499.6	1587.1	1587.0
T (°C)	32.8 ± 0.1	31.2 ± 0.1	28.3 ± 0.1
Salinity (ppt)	34.8	34.5	34.2
TAlk (µmol L^{-1})	NA	2408 ± 5	2390 ± 2
pH	8.17 ± 0.02	8.14 ± 0.02	8.11 ± 0.01
Calculated carbonate system parameters			
pCO_2 (uatm)	NA	295 ± 14	335 ± 17
HCO_3^- (mmol kg^{-1})	NA	1.61 ± 0.03	1.69 ± 0.02
CO_3^{2-} (mmol kg^{-1})	NA	0.30 ± 0.006	0.26 ± 0.006
DIC (mmol kg^{-1})	NA	1.93 ± 0.02	1.97 ± 0.02
Ω Aragonite	NA	5.02 ± 0.11	4.27 ± 0.10

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References

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823 Albright, R., Langdon, C., and Anthony, K.R.N.: (2013) Dynamics of seawater carbonate chemistry,
824 production, and calcification of a coral reef flat, central Great Barrier Reef, Biogeosciences, 10, 6747-
825 6758, https://doi.org/10.5194/bg-10-6747-2013, 2013.

826 Allgeier, J.E., Yeager, L.A. and Layman, C.A.: Consumers regulate nutrientlimitation regimes and
827 primary production in seagrass ecosystems, Ecology 94, 521–529, doi.org/ 10.1890/12-1122.1, 2013.

828 Allgeier, J.E., Layman, C.A., Mumby, P.J. and Rosemond, A.D.: Consistent nutrient storage and
829 supply mediated by diverse fish communities in coral reef ecosystems, Global Change Biology, 20,
830 2459–2472, doi.org/ 10.1111/gcb.12566, 2014.

831 Allgeier, J.E., Valdivia, A., Cox, C., and Layman, C.A.: Fishing down nutrients on coral reefs, Nature
832 Communications, 7, 1-5, doi.org/10.1038/ncomms12461, 2016.

833 Andersson A.J., and Gledhill D.: Ocean acidification and coral reefs: Effects on breakdown,
834 dissolution, and net ecosystem calcification, Annual Review of Marine Science, 5, 321–48,
835 https://doi.org/10.1146/annurev-marine-121211-172241, 2013.

836 Anthony, K.R.N., Kleypas, J.A., and Gattuso, J.P.: Coral reefs modify their seawater carbon
837 chemistry—implications for impacts of ocean acidification, Global Change Biology , 17, 3655–3666,
838 doi: 10.1111/j.1365-2486.2011.02510.x, 2011.

839 Atkinson, M.J.: Biogeochemistry of nutrients. In Coral Reefs: An ecosystem in transition, edited by:
840 Dubinsky, Z., and Stambler, N., Springer: London, 2011.

841 Bessey, C., Keesing, J.k., Mclaughlin, M.J., Rees, M., Tonks, M., Kendrick, G.A., and Olsen, Y.S.:
842 Teleost community composition and the role of herbivory on the intertidal reef of a small isolated
843 island in north-west Australia, Marine and Freshwater Research, 76, 684-696,
844 doi.org/10.1071/MF19066, 2020.

845 Blair, S.M., and Norris, J.N.: The deep-water species of Halimeda Lamouroux (Halimediaceae,
846 Chlorophyta) from San Salvador Island, Bahamas: species composition, distribution and depth
847 records, Coral Reefs, 6, 227–236, doi.org/10.1007/BF00302019, 1988.

848 Borowitzka, M.A., and Larkum, A.W.D.: Calcification in algae: Mechanisms and the role of
849 metabolism, Critical Reviews in Plant Sciences, 6, 1-45, doi.org/10.1080/07352688709382246, 1987.

850 Bruno, J.F. and Edmunds, P.J.: Metabolic consequences of phenotypic plasticity in the coral Madracis
851 mirabilis: the effect of morphology and water flow on aggregate respiration. Journal of Experimental
852 Marine Biology and Ecology, 229, 187–195, doi.org/10.1016/s0022-0981(98)00050-1, 1998.

853 Carlot, J., Rouzé, H., Barneche, D.R., Mercière, A., Espiau, B., Cardini, U., Brandl, S.J., Casey, J.M.,
854 Pérez-Rosales, G., Adjeroud, M., Hédouin, L., and Parravicini, V.: Scaling up calcification,
855 respiration, and photosynthesis rates of six prominent coral taxa, Ecology and Evolution, 12, e8613,
856 doi.org/10.1002/ece3.8613, 2022.

857 Carpenter, R.C., Hackney, J.M., and Adey, W.H.: Measurements of primary productivity and
858 nitrogenase activity of coral reef algae in a chamber incorporating oscillatory flow, Limnology and
859 Oceanography, 36, 40–49, doi.org/ 10.4319/lo.1991.36.1.0040, 1991.

860 Ceccarelli, D.M., Jones, G.P., and McCook, L.J.: Interactions between herbivorous fish guilds and
861 their influence on algal succession on a coastal coral reef, Journal of Experimental Marine Biology
862 and Ecology, 399, 60-67, doi.org/10.1016/j.jembe.2011.01.019, 2011.

Deleted: Barnes, D.J.: Profiling coral reef productivity and calcification using pH and oxygen electrodes, Journal of Experimental Marine Biology and Ecology, 66, 149–161, doi:10.1016/0022-0981(83)90036-9, 1983.¶
Barnes, D.J., and Lazar, B.: Metabolic performance of a shallow reef patch near Eilat on the Red sea, Journal of Experimental Marine Biology and Ecology, 174, 1–13, doi:10.1016/0022-0981(93)90248-M, 1993.¶

871 Chisholm, J.R.M., and Gattuso, J.-P.: Validation of the alkalinity anomaly technique for investigating
872 calcification of photosynthesis in coral reef communities, Limnology and Oceanography, 36, 1232-
873 1239, doi.org/10.4319/lo.1991.36.6.1232, 1991.

874 Cornwall, C.E., Comeau, S., Komder, N.A., Perry, C.T., van Hooidonk, R., DeCarlo, T.M., Pratchett,
875 M.S., Anderson, K.D., Browne, N., Carpenter, R., Diaz-Pulido, G., D'Olivo, J.P., Doo, S.S.,
876 Figueiredo, J., Fortunata, S.V.A., Kennedy, E., Lantz, C.A., McCulloch, M.T., Gonzalez-Rivero, M.,
877 Schoepf, V., Smithers, S.G., and Lowe, R.J.: Global declines in coral reef calcium carbonate
878 production under ocean acidification and warming, Proceedings of the National Academy of Sciences,
879 118, e2015265118, doi.org/10.1073/pnas.2015265118, 2021.

880 DeAngelis, D.L.: Dynamics of Nutrient Cycling and Food Webs: Chapman and Hall, London, 1992.

881 DeAngelis, D.L., Mulholland, P.J., Palumbo, A.V., Steinman, A.D., Huston, M.A. and Elwood, J.W.:
882 Nutrient dynamics and food-web stability, Annual Review of Ecology and Systematics, 20, 71–95,
883 www.jstor.org/stable/2097085, 1989.

884 Dickson, A., Gilmore, C.L., Christian, S., Christian, J.R. Guide to best practices for ocean CO2
885 measurements. North Pacific Marine Science Organization, 2007.

886 Doney, S.C., Fabry, V.J., Feely, R.A., and Kleypas, J.A.: Ocean acidification: the other CO2 problem,
887 Annual Review of Marine Science, 1, 169–192, doi.org/ 10.1146/annurev.marine.010908.163834,
888 2009.

889 Doughty, C.E. Roman, J., Faurbyd, S., Wolfe, A., Haquea, A., Bakkerf, E.S., Malhia, Y., Dunning
890 Jr.g, J.B., and Svenninget, J.-C.: Global nutrient transport in a world of giants. Procreedings of the
891 National Acadamy of Sciences USA, 113, 868–873, doi.org/ 10.1073/pnas.1502549112, 2015.

892 Drew, E.A.: Halimeda biomass, growth rates and sediment generation on reefs in the central great
893 barrier reef province, Coral Reefs, 2, 101-110, doi.org/10.1007/BF02395280, 1983.

894 Eakin, C.M.: Where have all the carbonates gone? A model comparison of calcium carbonate budgets
895 before and after the 1982–1983 El Nino at Uva Island in the eastern Pacific, Coral Reefs, 15, 109-119,
896 doi.org/10.1007/BF01771900, 1996.

897 Frankignoulle, M., Gattuso, J.P., Biondo, R., Bourge, I., CopinMontegut, G., and Pichon, M.: Carbon
898 fluxes in coral reefs II: eulerian study of inorganic carbon dynamics and measurement of air-sea CO_2
899 exchanges, Marine Ecology Progress Series, 145, 123–132, doi:10.3354/meps145123, 1996.

900 Freile, D., Milliman, J.D., and Hillis, L.: Leeward bank margin Halimeda meadows and draperies and
901 their sedimentary importance on the western Great Bahama Bank slope, Coral Reefs, 14, 27-33,
902 doi.org/10.1007/BF00304068, 1995.

903 Gattuso, J.-P., Pichon, M., Delesalle, B., and Frankignoulle, M.: Community metabolism and airsea
904 CO_2, fluxes in a coral reef ecosystem (Moorea, French Polynesia). Marine Ecology Progress Series,
905 96, 259-267, http://www.jstor.org/stable/24833554, 1993.

906 Gattuso, J.-P., Pichon, M., and Frankignoulle, M.: Biological control of air-sea CO2 fluxes: Effect of
907 photosynthetic and calcifying marine organisms and ecosystems. Marine Ecology Progress Series,
908 129, 307- 312, doi.org/10.3354/meps129307, 1995.

909 Gattuso, J.-P., Frankignoulle, M., Smith, S.V., Ware, J.R., and Wollast, R.: Coral reefs and carbon
910 dioxide. Science, 271, 1298, doi.org/10.1126/science.271.5253.1298-a, 1996a.

911 Gattuso, J.-P., Pichon, M., Delesalle, B., Canon, C., and Frankignoulle, M.: Carbon fluxes in coral
912 reefs I: lagrangian measurement of community metabolism and resulting air-sea CO2 disequilibrium,
913 Marine Ecology Progress Series, 145, 109–121, doi:10.3354/meps145109, 1996b.

Deleted: Done, T.: Phase shifts in coral reef communities and their ecological signicance. Hydrobiologica, 247, 121–132, doi.org/10.1007/BF0000821, 1992.¶

Deleted: Duarte, C.M., Hendriks, I.E., Moore, T.S., Olsen, Y.S., Steckbauer, A., Ramajo, L., Carstensen, J., Trotter, J.A., and McCulloch, M.: Is Ocean Acidification an Open-Ocean Syndrome? Understanding Anthropogenic Impacts on Seawater pH, Estuaries and Coasts, 36, 221-236, doi.org/ 10.1007/s12237-013-9594-3, 2013.¶

922 Gattuso, J.-P., Payri, C.E., Pichon, M., Delesalle, B., and Frankignoulle, M.: Primary production,
923 calcification, and air-sea CO2 fluxes of a macroalgal dominated coral reef community (Moorea,
924 French Polynesia), Journal of Phycology, 33, 729-738, doi.org/ 10.1111/j.0022-3646.1997.00729.x,
925 1997.

926 Gattuso, J.-P., Epitalon, J.-M., Orr, J., Gentili, B., Hagens, M., Hofmann, A., Mueller, J.-D., Proye,
927 A., Rae, J., and Soetaert, K.: seacarb:Seawater Carbonate Chemistry, 2018.

928 Gilmour, J.P., Smith, L.D., Heyward, A.J., Baird, A.H., and Pratchett, M.S.: Recovery of an Isolated
929 Coral Reef System Following Severe Disturbance, Science, 340, 69-71, doi.org/
930 10.1126/science.1232310, 2013.

931 Halpern, B.S., Walbridge, S., Selkoe, K.A., Kappel, C.V., Micheli, F., Agrosa, C., Bruno, J.F., Casey,
932 K.S., Ebert, C., Fox, H.E., Fujita, R., Heinemann, D., Lenihan, H.S., Madin, E.M.P., Perry, M.T.,
933 Selig, E.R., Spalding, M., Steneck, R., and Watson, R.: A Global Map of Human Impact on Marine
934 Ecosystems, Science, 319, 948, doi.org/ 10.1126/science.1149345, 2008.

935 Halpern, B.S., Frazier, M., Afflerbach, J., Lowndes, J.S., Micheli, F., O'Hara, C., Scarborough, C.,
936 and Selkoe, K.A.: Recent pace of change in human impact on the world's ocean, Science Reports, 9,
937 11609, doi.org/10.1038/s41598-019-47201-9, 2019.

938 Harborne, A.R., Rogers, A., Bozec, Y.-M. and Mumby, P.J.: Multiple stressors and the functioning of
939 coral reefs. Annual Review of Marine Science, 9, 445–468, 2017.

940 Harley, C. D., Hughes, A.R., Hultgren, K.M., Miner, B.J., Sorte, C.J.B., Thornber, C.S., Rodriguez,
941 L.F., Tomanek, L., Williams S.L.: The impacts of climate change in coastal marine systems, Ecology
942 Letters, 9, 228– 241, doi.org/10.1111/j.1461-0248.2005.00871.x, 2006.

943 Hart, D.E., and Kench, P.S.: Carbonate production of an emergent reef platform, Warraber Island,
944 Torres Strait, Australia, Coral Reefs, 26, 53-68, doi.org/ 10.1007/s00338-006-0168-8, 2007.

945 Hatcher, B.G.: Coral reef primary productivity–a hierarchy of patterns and process. Trends in Ecology
946 and Evolution, 5, 149–155, doi.org/10.1016/0169-5347(90)90221-X, 1990.

947 Hewitt, J.E., Ellis, J.I., and Thrush, S.F.: Multiple stressors, nonlinear effects and the implications of
948 climate change impacts on marine coastal ecosystems, Global Change Biology, 2, 2665–2675.
949 doi.org/10.1111/gcb.13176, 2016.

950 Heyward, A., Jones, R., Meeuwig, J., Burns, K., Radford, B., Colquhoun, J., Cappo, M., Case, M.,
951 O'Leary, R., Fisher, R., Meekan, M., and Stowar, M.: Monitoring Study S5. Banks and Shoals,
952 Montara 2011 Offshore Banks Assessment Survey Report for PTTEP Australasia (Ashmore Cartier)
953 Pty. Ltd., Australian Institute of Marine Science, Townsville, 253pp, 2011.

954 Hoegh-Guldberg, O., Mumby, P. J., Hooten, A. J., Steneck, R. S., Greenfield, P., Gomez, E., Harvell,
955 C. D., Sale, P. F., Edwards, A. J., Caldeira, K., Knowlton, N., Eakin, C. M., Iglesias-Prieto, R.,
956 Muthiga, N., Bradbury, R. H., Dubi, A., and Hatziolos, M. E.: Coral reefs under rapid climate change
957 and ocean acidification, Science, 318, 1737–1742, doi.org/10.1126/science.1152509, 2007.

958 Houlbreque, F., and Ferrier-Pages, C.: Heterotrophy in tropical scleractinian corals, Biological
959 reviews of the Cambridge Philosophical Society, 84, 1-17, doi.org/10.1111/j.1469-
960 185X.2008.00058.x, 2009.

961 Houlbreque, F., Tambutte, E., Allemand, D. and Ferrier-Pages, C.: Interactions between zooplankton
962 feeding, photosynthesis and skeletal growth in the Scleractinian coral Stylophora pistillata, Journal of
963 Experimental Biology, 207, 1461–1469, doi.org/10.1242/jeb.00911, 2004.

Deleted: Gattuso, J.-P., Allemand, D., and Frankignoulle, M.: Photosynthesis and calcification at cellular, organismal and community levels in coral reefs: A review on interactions and control by carbonate chemistry, American Zoologist, 39, 160-183, doi.org/10.1093/icb/39.1.160, 1999.¶

Deleted: Hatcher, B.G.: Coral reef ecosystems: How much greater is the whole than the sum of the parts? Coral Reefs, 16, 77–91, doi.org/10.1007/s003380050244, 1997.¶

972   Hudson, J.H.: Growth rate and carbonate production in Halimeda opuntia: Marquesas Keys, Florida.
973   In Paleoalgology: contemporary research and applications, edited by Toomey, D.F. and Nitecki,
974   M.H., Springer-Verlag: Berlin, 1985.

975   Hughes, T.P., Kerry, J.T., Álvarez-Noriega, M., Álvarez-Romero, J.G., Anderson, K.D., Baird, A.H.,
976   Babcock, R.C., Beger, M., Bellwood, D.R., Berkelmans, R., Bridge, T.C., Butler, I.R., Byrne, M.,
977   Cantin, N.E., Comeau, S., Connolly, S.R., Cumming, G.S., Dalton, S.J., Diaz-Pulido, G., Eakin, C.M.,
978   Figueira, W.F., Gilmour, J.P., Harrison, H.B., Heron, S.F., Hoey, A.S., Hobbs, J.A., Hoogenboom,
979   M.O., Kennedy, E.V., Kuo, C.-Y., Lough, J.M., Lowe, R.J., Liu, G., McCulloch, M.T., Malcolm,
980   H.A., McWilliam, M.J., Pandolfi, J.M., Pears, R.J., Pratchett, M.S., Schoepf, V., Simpson, T.,
981   Skirving, W.J., Sommer, B., Torda, G., Wachenfeld, D.R., Willis, B.L. and Wilson, S.K.: Global
982   warming and recurrent mass bleaching of corals, Nature, 543, 373–377, doi.org/10.1038/nature21707,
983   2017a.

984   Hughes, T.P., Barnes, M.L, Bellwood, D.R., Cinner, J.E., Cumming, G.S., Jackson, J.B.C., Kleypas,
985   J., van de Leemput, I.A., Lough, J.M., Morrison, T.H., Palumbi, S.R., van Nes, E.H. and Scheffer, M.:
986   Coral reefs in the Anthropocene, Nature, 546, 82-90, doi:10.1038/nature22901, 2017b.

987   IPCC: Climate Change 2014: Impacts, Adaptation, and Vulnerability, Part A: Global and Sectoral
988   Aspects, Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental
989   Panel on Climate Change, Cambridge University Press, Cambridge, United Kingdom and New York,
990   2014.

991   Jokiel, P.L.: Ocean Acidification and Control of Reef Coral Calcification by Boundary Layer
992   Limitation of Proton Flux, Bulletin of Marine Science, 87, 639-657, doi.org/10.5343/bms.2010.1107,
993   2011.

994   Kangwe, J., Semesi, I.S., Beer, S., Mtolera, M., and Björk, M.: Carbonate Production by Calcareous
995   Algae in a Seagrass-Dominated System: The Example of Chwaka Bay, CHAPTER 8, In People,
996   Nature and Research in Chwaka Bay, Zanzibar, Tanzania, edited by de la Torre-Castro, M. and
997   Lyimo, T.J., WIOMSA: Zanzibar, 2012.

998   Kayanne, H., Suzuki, A., and Saito, H.: Diurnal changes in the partial pressure of carbon dioxide in
999   coral reef water, Science, 269, 214—216, doi.org/ 10.1126/science.269.5221.214, 1995.

1000   Kinsey, D.W.: Metabolism, calcification and carbon production: I:System level studies, paper
1001   presented at 5th International Coral Reef Congress, Int. Coral Reef Soc., Tahiti, 1985.

1002   Kleypas, J.A., and Yates, K.K.: Coral reefs and ocean acidification, Oceanography, 22, 108–117,
1003   https://doi.org/10.5670/oceanog.2009.101, 2009.

1004   Lesser, M.P., Weis, V.M., Patterson, M.R., and Jokiel, P.L.: Effects of morphology and water motion
1005   on carbon delivery and productivity in the reef coral, Pocillopora damicornis: diffusion barriers,
1006   inorganic carbon limitation, and biochemical plasticity, Journal of Experimental Marine Biology and
1007   Ecology, 178, 153–179, doi.org/10.1016/0022-0981(94)90034-5, 1994.

1008   Lewis, J. B.: Process of organic production on coral reefs, Biolocial Review, 52, 305–347,
1009   doi.org/10.1111/j.1469-185X.1977.tb00836.x, 1977.

1010   Lowe, R.J., Leon, A.S., Symonds, G., Falter, J.L., and Gruber, R.: The intertidal hydraulics of tide-
1011   dominated reef platforms, J. Geophys. Res.-Oceans, 120, 4845–4868,
1012   https://doi.org/10.1002/2015jc010701, 2015.

1013   Madin, J.S., Anderson, K.D., Andreasen, M.H., Bridge, T.C.L., Cairns, S.D., Connolly, S.R., Darling,
1014   E.S., Diaz, M., Falster, D.S., Franklin, E.C., Gates, R.D., Harmer, A.M.T., Hoogenboom, M.O.,
1015   Huang, D., Keith, S.A., Kosnik, M.A., Kuo, C.-Y., Lough, J.M., Lovelock, C.E., Luiz, O., Martinelli,

Deleted: Kayanne, H., Hata,H., Kudo, S., Yamano, H., Watanabe,A., Ikeda, Y., Nozaki, K., Kato, K., Negishi, A., and Saito, H.: Seasonal and bleaching-induced changes in coral reef metabolism and CO2 flux, Global Biogeochemical Cycles, 19, 1– 11, doi.org/10.1029/2004GB002400, 2005.¶

Deleted: Kleypas, J.A., Anthony, K.R.N., and Gattuso, J.P.: Coral reefs modify their seawater carbon chemistry—case study from a barrier reef (Moorea, French Polynesia), Global Change Biology, 17, 3667–3678, doi.org/10.1111/j.1365-2486.2011.02530.x, 2011.¶

1025 J., Mizerek, T., Pandolfi, J.M., Pochon, X., Pratchett, M.S., Putnam, H.M., Roberts, T.E., Stat, M.,
1026 Wallace, C.C., Widman, E. and Baird, A.H.: The Coral Trait Database, a curated database of
1027 trait information for coral species from the global oceans. Scientific Data, 3, 160017.
1028 https://doi.org/10.1038/sdata. 2016.

1029 Mass, T., Genin, A., Shavit, U., Grinstein, M., and Tchernov, D.: Flow enhances photosynthesis in
1030 marine benthic autotrophs by increasing the efflux of oxygen from the organism to the water,
1031 Proceedings of the National Academy of Sciences USA, 107, 2527–2531,
1032 doi.org/10.1073/pnas.0912348107, 2010.

1033 McLaughlin M.J., Lourey M.J., Hanson C.E.., Cherukuru N, Thompson P.A., and Pattiaratchi C.:
1034 Biophysical oceanography of tidally-extreme waters of the southern Kimberley coast, Western
1035 Australia, Continental Shelf Research, 173, 1-12, doi.org/10.1016/j.csr.2018.12.002, 2019.

1036 Meyer, J.L., Schultz, E.T. and Helfman, G.S.: Fish schools–an asset to corals, Science 220, 1047–
1037 1049, doi.org/ 10.1126/science.220.4601.1047, 1983.

1038 Moberg F., and Folke C.: Ecological goods and services of coral reef ecosystems, Ecological
1039 Economics, 29, 215–233, doi.org/10.1016/S0921-8009(99)00009-9, 1999.

1040 Montaggioni, L.F., and Braithwaite, C.J.R.: Quaternary coral reef systems. Elsevier, p 532, 2009.

1041 Moore, J.A.Y., Bellchambers, L.M., Depczynski, M.R., Evans, R.D,, Evans, S.N., Field, S.N.,
1042 Friedman, K.J., Gilmour, J.P., Holmes, T.H., Middlebrook, R., Radford, B.T., Ridgway, T., Shedrawi,
1043 G., Taylor, H., Thomson, D.P., & Wilson, S.K. Unprecedented Mass Bleaching and Loss of Coral
1044 across 12°of Latitude in Western Australia in 2010–11. PLoS ONE 7(12): e51807.
1045 doi:10.1371/journal.pone.0051807, 2012.

1046 Nelson, W.A.: Calcified macroalgae – critical to coastal ecosystems and vulnerable to change: a
1047 review, Marine and Freshwater Research, 60, 787–801, doi.org/ 10.1071/MF08335, 2009.

1048 Olsen, Y.S., Bessey, C., McLaughlin, J., and Keesing, J.K.: Annual Report: Patterns in primary
1049 producers, herbivory and reef metabolism around Browse Island, Milestone Report for Shell/INPEX
1050 Applied Research Program, 2017.

1051 Overholtzer, K.L. and Motta, P.J.: Comparative resource use by juvenile parrotfishes in the Florida
1052 Keys, Marine Ecology Progress Series, 177, 177−187, 1999.

1053 Panchang, R. and Ambokar, M.: Ocean acidification in the Northern Indian ocean : A review, Journal
1054 of Asian Earth Sciences, doi.org/10.1016/j.jseaes.2021.104904, 219, (104904), 2021.

1055 Payri, C.E.: Halimeda contribution to organic and inorganic production in a Tahitian reef system,
1056 Coral Reefs, 6, 251-262, doi.org/10.1007/BF00302021, 1988.

1057 Perry, C.T., Spencer, T., and Kench, P.: Carbonate budgets and reef production states: a geomorphic
1058 perspective on the ecological phase-shift concept, Coral Reefs, 27, 853–866, doi.org/10.1007/s00338-
1059 008-0418-z, 2008.

1060 Perry, C.T., Edinger, E.N., Kench, P.S., Murphy, G.N., Smithers, S.G., Steneck, R.S., and Mumby,
1061 P.J.: Estimating rates of biologically driven coral reef framework production and erosion: a new
1062 census-based carbonate budget methodology and applications to the reefs of Bonaire, Coral Reefs, 31,
1063 853–868, doi.org/ 10.1007/s00338-012-0901-4, 2012.

1064 Perry, C.T., Alvarez-Filip, L., Graham, N.A.J., Mumby, P.J., Wilson, S.K., Kench, P.S., Manzello,
1065 D.P., Morgan, K.M., Slangen, A.B.A., Thomson, D.P., Januchowski-Hartley, F., Smithers, S.G.,
1066 Steneck, R.S., Carlton, R., Edinger, E.N., Enochs, I.C., Estrada-Saldívar, N., Haywood, M.D.E.,
1067 Kolodziej, G., Murphy, G.N., Pérez-Cervantes, E., Suchley, A., Valentino, L., Boenish, R., Wilson,

Deleted: Murru, M., and Sandgren, C.D.: Habitat matters for inorganic carbon acquisition in 38 species of red macroalgae (Rhodophyta) from Puget Sound, Washington, USA, Journal of Phycology, 40, 837–845, doi.org/10.1111/j.1529-8817.2004.03182.x, 2004.¶

Deleted: Niggel, W., Haas, A.F., and Wild, C.: Benthic community composition affects O2 availability and variability in a Northern Red Sea fringing reef, Hydrobiologia, 644, 401–405, doi.org/10.1007/s10750-010-0200-4, 2010.¶
Odum, H. T., and Odum, E. P.: Trophic structure and productivity of a windward coral reef community on Eniwetok Atoll, Ecological Monographs, 25, 291–320, 1955.¶

Deleted: Pandolfi, J. M., Connolly, S. R., Marshall, D. J., and Cohen, A. L.: Projecting coral reef futures under global warming and ocean acidification, Science, 333, 418–422, doi.org/10.1126/science.1204794, 2011.¶

M., and Macdonald, C.: Loss of coral reef growth capacity to track future increases in sea level. Nature, 558, 396–400, doi.org/10.1038/s41586-018-0194-z, 2018.

Pomeroy, L.R.: The ocean's food web, a changing paradigm. Bioscience 24, 9, doi.org/10.2307/1296885, 1974.

Price, N.N., Hamilton, S.L., Tootell, J.S., and Smith, J.E.: Species-specific consequences of ocean acidification for the calcareous tropical green algae *Halimeda,* Marine Ecology Progress Series, 440, 67–78, doi.org/10.3354/meps09309, 2011.

R Core Team. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/. 2018.

Rees, S.A., Opdyke, B.N., Wilson, P.A., and Henstock, T.J.: Significance of Halimeda bioherms to the global carbonate budget based on a geological sediment budget for the Northern Great Barrier Reef, Australia, Coral Reefs, 26, 177-188, doi.org/10.1007/s00338-006-0166-x, 2007.

Richards, Z.T., Garcia, R.A., Wallace, C.C., Rosser, N.L., and Muir, P.R.: A diverse assemblage of reef corals thriving in a dynamic intertidal reef setting (Bonaparte Archipelago, Kimberley, Australia), PLoS ONE, 10, e0117791, doi.org/10.1371/journal.pone.0117791, 2015.

Rueden, C.T., Schindelin, J., Hiner, M.C., DeZonia, B.E., Walter, A.E., Arena, E.T., and Eliceiri, K.W.: ImageJ2: ImageJ for the next generation of scientific image data, BMC Bioinformatics, 18, 529, doi.org/10.1186/s12859-017-1934-z, 2017.

Schindler, D.W.: Recent advances in the understanding and management of eutrophication, Limnology and Oceanography, 51, 356– 363, doi.org/ 10.4319/lo.2006.51.1_part_2.0356, 2006.

Shaw, E.C., Hamylton, S.M., and Phinn, S.R.: Incorporating benthic community changes into hydrochemical-based projections of coral reef calcium carbonate production under ocean acidification, Coral Reefs, 35, 739-750, doi.org/10.1007/s00338-016-1407-2, 2016.

Silverman, J., Lazar, B., Cao, L., Caldeira, K., and Erez, J.: Coral reefs may start dissolving when atmospheric CO2 doubles, Geophysical Research Letters, 36, L05606, doi:10.1029/2008gl036282, 2009.

Smith, J.E., Hunter, C.L., Conklin, E.J., Most, R., Sauvage, T., Squair, C., and Smith, C.M.: Ecology of the Invasive Red Alga Gracilaria salicornia (Rhodophyta) on O'ahu, Hawai'i, Pacific Science, 58, 325-343, doi.org/ 10.1353/psc.2004.0023, 2004.

Smith, J.E., Price, N.N., Nelson, C.E., and Haas, A.F. Coupled changes in oxygen concentration and pH caused by metabolism of benthic coral reef organisms, Marine Biology, 160, 2437-2447, doi.org/10.1007/s00227-013-2239-z, 2013.

Smith, S.V., and Key, G.S.: Carbon dioxide and metabolism in marine environments, Limnology and Oceanography, 20, 493-495, doi.org/10.4319/lo.1975.20.3.0493, 1975

Smith, S.V.: Reflections on the measurement and significance of carbon metabolism on coral reefs, Kansas Geological Survey Open-File Report 95-96a, Kansas Geological Survey, Lawrence, Kansas, 1995.

Smith, T.B., Nemeth, R.S., Blondeau, J., Calnan, J.M., Kadison, E., and Herzlieb S.: Assessing coral reef health across onshore to offshore stress gradients in the US Virgin Islands, Marine Pollution Bulletin, 56, 1983–1991, doi.org/10.1016/j.marpolbul.2008.08.015, 2008.

1146   Sorokin, Y.: in Coral Reef Ecology, 102, 215–249, edited by: Heldmaier, G., Lange, O.L., Mooney,
1147   H.A., and Sommer, U., Springer: Berlin, Heidelberg, 1995.

1148   Sreeush, M.G., Valsala, V., Santanu, H., Pentakota, S., Prasad, K.V.S.R., Naidu, C.B., and
1149   Murtugudde, R.: Biological production in the Indian Ocean upwelling zones – Part II: Data based
1150   estimates of variable compensation depths for ocean carbon mdels via Cyclostationary Bayesian
1151   Inversion, Deep Sea Research Part II, 179, doi.org/10.1016/j.dsr2.2019.07.007, 2020.

1152   Stuart-Smith, R.D., Brown, C.J., Ceccarelli, D.M. and Edgar, G.J.: Ecosystem restructuring along the
1153   Great Barrier Reef following mass coral bleaching, Nature, 560, 92–96, 2018.

1154   Szmant, A.M.: Nutrient enrichment on coral reefs: is it a major cause of coral reef decline? Estuaries
1155   25, 743–766, doi.org/10.1007/BF02804903, 2002.

1156   Trapon, M.L., Pratchett, M.S., and Hoey, A.S.: Spatial variation in abundance, size and orientation of
1157   juvenile corals related to the biomass of parrotfishes on the Great Barrier Reef, Australia, PLoS One,
1158   8, e57788, doi.org/10.1371/journal.pone.0057788, 2013.

1159   Veal, C.J., Carmi, M., Fine, M., and Hoegh-Guldberg, O.: Increasing the accuracy of surface area
1160   estimation using single wax dipping of coral fragments, Coral Reefs, 29, 893-897,
1161   doi.org/10.1007/s00338-010-0647-9, 2010.

1162   Vecsei, A.: A new estimate of global reefal carbonate production including the fore-reefs. Global
1163   Planet Change, 43, 1–18, doi.org/10.1016/j.gloplacha.2003.12.002, 2004.

1164   Vroom, P.S., Smith, C.M., Coyer, J.A. Walters, L.J., Hunter, C.L., Beach, K.S., & Smith, J.E.: Field
1165   biology of Halimeda tuna (Bryopsidales, Chlorophyta) across a depth gradient: comparative growth,
1166   survivorship, recruitment, and reproduction. Hydrobiologia, 501, 149–166,
1167   https://doi.org/10.1023/A:1026287816324, 2003.

1168   Walther, G-R.: Community and ecosystem responses to recent climate change, Philosophical
1169   Transactions of the Royal Society B: Biological Sciences, 365, 2019– 2024, doi.org/
1170   0.1098/rstb.2010.0021, 2010.

1171   Watson, R.J., Butler, E.C.V., Clementson, L.A., and Berry, K.M.: Flow-injection analysis with
1172   fluorescence detection for the determination of trace levels of ammonium in seawater, Journal of
1173   Environmental Monitoring, 7, 37-42, doi.org/10.1039/b405924g, 2005.

1174   Ware, J. R., Smith, S.V., and Reaka-Kudla, M.L.: Coral reefs: Sources or sinks of atmospheric CO2?
1175   Coral Reefs, 11, 127-130, doi.org/10.1007/BF00255465, 1992.

1176   WillyWeather 2022, Browse Island Sunrise / Sunset Times website, accessed 02 November 2022,
1177   <https://sunrisesunset.willyweather.com.au/wa/kimberley/browse-island.html>.

1178

Deleted: Venn, A. A., Tambutté, E., Holcomb, M., Laurent J., Allemand, D. and Tambutté, S.: Impact of seawater acidification on pH at the tissue–skeleton interface and calcification in reef corals, Proceedings of the National Academy of Sciences, 110, 1634–1639, doi.org/10.1073/pnas.1216153110, 2013.¶

Deleted: Wild, C., Niggel, W., Naumann, M.S., and Haas, A.F.: Organic matter release by Red Sea coral reef organisms—potential effects on microbial activity and in situ O2 availability, Marine Ecology Progress Series, 411, 61–71, doi.org/10.3354/meps08653, 2010.¶

Deleted: Zeebe, R.E., Wolf-Gladrow, D.A., and Jansen, H.: On the time required to establish chemical and isotopic equilibrium in the carbon dioxide system in seawater, Marine Chemistry, 65, 135–153, doi.org/10.1016/S0304-4203(98)00092-9, 1999.¶